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Research Article

Trophic interactions between the European pond turtle (*Emys orbicularis*) and invasive non-native species

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Abstract

Biological invasions contrast with reintroduction projects, where native species are deliberately returned to their natural habitat to restore local biodiversity. Such a reintroduction project is being carried out in the Upper Rhine Valley with the European pond turtle (*Emys orbicularis*) in the transbordering region between Lauterbourg (France) and Neuburg am Rhein (Germany), hereafter referred as Neu-Woerr. Several ponds have been created to benefit the dispersal of reintroduced turtles. However, this pondscape has been recently widely invaded by the calico crayfish (*Faxonius immunis*) and partly by the zebra mussel (*Dreissena polymorpha*). These two invasive non-native species decrease the overall habitat quality due to the massive exploitation of phytoplankton by the zebra mussel as well as macrophytes and macroinvertebrates by the calico crayfish. However, these invasive non-native species are also potential novel prey for the reintroduced turtles. Here, we investigated the trophic interactions under captive conditions between the turtle and the two invasive non-native species. We conducted prey choice tests of turtles with calico crayfish of different sex, size, and shell hardness, as well as with zebra mussels of different size. Additionally, faecal samples of wild caught turtles on Neu-Woerr were sampled and analysed for calico crayfish DNA. Our results demonstrated that the turtles were capable of preying on the calico crayfish in the wild and in captivity, preferring small crayfish individuals, with no sexual preference for the less aggressive female crayfish. For the zebra mussels, turtles preyed preferably on small alive individuals, while they also preyed on larger, yet dead mussels. This study provides new insights into the feeding ecology of the European pond turtle and highlights added benefits and values of reintroduction projects when the reintroduced species additionally acts as a novel predator of invasive species.

Key words: Biological invasions, calico crayfish, eDNA, environmental genomics, foraging behaviour, prey choice, zebra mussel

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Introduction

Invasive non-native species (*sensus* Soto et al. 2024) are among the largest threats to biodiversity (Keller et al. 2011; Bellard et al. 2016) in addition to the threats posed by habitat loss, climate change, overexploitation, and pollution (IPBES 2019;

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Prakash and Verma 2022). Freshwater ecosystems are particularly threatened by invasive species (Sala et al. 2000; Abell 2002). Moreover, negative ecological and economic impacts are more likely and more difficult to detect in freshwater than in terrestrial ecosystems (Moorhouse and Macdonald 2014; Thomaz et al. 2015). Furthermore, the rapid spread of larvae and seeds facilitated by the water current or boats leads to a high rate of invasion and a widespread distribution (Genovesi 2007). Sensitive and rare freshwater ecosystems, such as marshland and floodplains, are additionally severely affected by human made degradation (Tickner et al. 2020), leading to overexploited and unbalanced ecosystems (e.g., Bromberg Gedan et al. 2009; Entwistle et al. 2019). In such disturbed ecosystems invasive species can thrive due to, e.g., vacant ecological niches or the lack of natural predators (Keller et al. 2011; Haubrock et al. 2020).

The calico crayfish (*Faxonius immunis* Hagen, 1870) originates from North America and was found in Europe for the first time in 1993 in Schiftung, Germany, close to the Upper Rhine (Gelmar et al. 2006). At present, the main distribution area of this non-native crayfish with high population densities is still along the Upper Rhine in Western Germany and Northeastern France (Gelmar et al. 2006; Collas et al. 2012; Herrmann et al. 2018a; Marie et al. 2019). However, the species seems to be spreading further downstream the Rhine, as it has recently been detected in Hesse (Herrmann et al. 2018b), North Rhine-Westphalia (Groß 2019) and the Netherlands (Ottburg et al. 2019). Its rapid life cycle, characterised by reaching sexual maturity already in the first summer (Chucholl 2012), its very high fecundity and its ability to live in both stagnant and flowing waters (Gelmar et al. 2006) promote the high invasive potential of the calico crayfish. Moreover, the calico crayfish is, like most crayfish of North American origin, a latent carrier of a specific strain of the crayfish plague pathogen (*Aphanomyces astaci* Schikora, 1906; Jussila et al. 2021) of high virulence (Francesconi et al. 2024), which in addition to its aggressiveness (Chucholl et al. 2008) supports its potential as a competitor for the native crayfish fauna (Chucholl 2012), e.g., the stone crayfish (*Austropotamobius torrentium* Schrank, 1803; Chucholl 2016). The calico crayfish has the habit to excavate burrows in the mud where it retreats itself during dryness, allowing it to survive long periods in drained or frozen water bodies (Ott 2014). According to Chucholl (2012), it is a polytrophic omnivore feeding on detritus, macrophytes and macroinvertebrates, with Cladocera and larvae of Chironomidae and Ephemeroptera being its most common prey. Further, the calico crayfish exerts a large *per capita* impact on gammarids (Chucholl and Chucholl 2021). This feeding behaviour is particularly problematic in small, isolated water bodies where large fish are lacking as predators (Dorn et al. 1999; Reynolds 2011). In such small ponds, the calico crayfish can establish itself due to its wide tolerance to temperature and oxygen conditions and establish large populations (Tack 1941; Wiens and Armitage 1961). Under these conditions, the calico crayfish can cause major ecological devastation (Ott 2014; Herrmann et al. 2022) and leave behind a turbid water due to its highly destructive burying activities (Martens 2016).

The zebra mussel (*Dreissena polymorpha* Pallas, 1771) is a freshwater bivalve mollusc that originates from the Ponto-Caspian region which stretches between the Black Sea and the Caspian Sea. Its spread to Central and Western Europe started at the beginning of the 19th century through an expanding canal system connecting Russian rivers to those in Europe (Bij de Vaate et al. 2002; Jernelöv 2017; Haubrock et al. 2024). Accordingly, the Upper Rhine Valley has been subject to zebra mussel

invasion for several decades now (Bernauer and Jansen 2006; Soto et al. 2023; Karatayev and Burlakova 2025). This species consumes high amounts of phytoplankton, which can lead to changes in water clarity, productivity, and heat budget of lakes (Zaiko and Olenin 2009; Higgins and Vander Zanden 2010; Woodruff et al. 2021). Further, zebra mussels compete with native unionids for food and attach themselves in high density to unionid bivalve molluscs, preventing local unionids from feeding, moving and burrowing (Karatayev et al. 1997; Aldridge et al. 2004; Sousa et al. 2010). Additionally, the zebra mussel competitiveness and invasiveness are enhanced by its high fecundity (30,000–40,000 eggs), its highly mobile propagules, its wide temperature (-2 °C–40 °C) and salinity (0.007–14‰) tolerance, its compliance to low oxygen levels for several days, and its capacity to survive up to three weeks out of water (Khalanski 1997; Zaiko and Olenin 2009; Pollux et al. 2010). Besides its ecological impacts, the zebra mussel can damage pipes and water filtration plants as well as water turbines (Pimentel et al. 2005), with significant impacts on the freshwater industry, agriculture, and municipal drinking-water supply and causes high economic costs (Waller et al. 2021; Haubrock et al. 2022).

In the Upper Rhine Valley, high densities of calico crayfish and zebra mussel (Grac et al. 2015; Herrmann et al. 2022) may severely alter the aquatic habitat and food web. In the transbordering region of Northeastern France and Southwestern Germany (hereafter referred as Neu-Woerr; Georges and Theissinger 2023), where wetlands have been restored and a new pondscape created for the European pond turtle (*Emys orbicularis* Linnaeus, 1758) reintroduction (Quintard and Georges 2023; Philippot and Georges 2023), these invasive non-native species may thus have indirect impacts on the success of such conservation efforts. Various approaches to eradicate invasive crayfish or mussels have been previously tested, using chemical pesticides (Strayer 2009), biological pesticides (Waller and Bartsch 2018) or intensive trapping (Piazza et al. 2014; Green et al. 2020). Yet these methods have not been proven to be widely applicable, because they cause unwanted lethal effects on nontarget native species or exert insufficient pressure to eliminate large populations of target invasive species (Strayer 2009; Peay et al. 2019; Oliver et al. 2021). Nevertheless, if no eradication is possible, it is of upmost importance to at least control the population of invasive species (Pyšek et al. 2020). One possibility is biological control by natural predators.

The European pond turtle could be a possible natural predator of invasive invertebrates. This small sized turtle is an opportunistic feeder preying mainly on aquatic macroinvertebrates (e.g., gastropods, arthropods), in addition to seeds and plants (Ottonello et al. 2018; Quintard and Georges 2023; Rahimibashar et al. 2024; Meyer et al. in press). Faecal analyses in other studies have already shown that the turtle also preys on larger animals such as the red swamp crayfish (*Procambarus clarkii* Girard, 1852; Ottonello et al. 2005), whereas mussels have so far appeared to be more accidental prey in the wild (Ziane et al. 2020). However, food composition and frequency also depend heavily on the region and the season, and thus on prey availability (Çiçek and Ayaz 2011). The European pond turtle acts as a native umbrella species in numerous reintroduction projects throughout Europe, including the biodiversity hotspot of the Upper Rhine Valley. Such reintroduction projects aim to counteract the general trend of biodiversity erosion in wetlands and may provide beneficial services against non-native species through the predatory behaviour of the European pond turtle. However, the trophic interactions between the European pond turtle and the invasive

calico crayfish and the zebra mussel have not been assessed yet. It is of high importance to investigate where these two invasive non-native species are placed within the wetland food web and how they are ecologically linked to the natural occurring species (van der Putten et al. 2004; Genovesi 2007). Depending on whether these non-native species serve as potential new prey for organisms of a higher trophic level or, conversely, as new predators for lower trophic levels, or both, they can have varying impacts on the food web and the entire ecosystem. The knowledge about trophic interactions between newly reintroduced European pond turtles and newly settled invasive calico crayfish and zebra mussels in the Upper Rhine Valley is therefore fundamental for management plans and the protection of reintroduced species and the entire ecosystem.

In this study we investigated for the first time the possible trophic interactions between the native reintroduced European pond turtle and the invasive calico crayfish and the zebra mussel. The main question was whether turtles can prey on these non-native invertebrates, and if so, what are the characteristics of the turtles' preying and feeding behaviour. To investigate this, turtle faecal samples were collected after capturing in the wild, for subsequent DNA isolation to detect calico crayfish DNA. Further, prey-choice tests were conducted with captive turtles and crayfish as well as mussels of different size classes. We hypothesised that the exoskeleton and shell of small-sized calico crayfish and zebra mussels, respectively, can be broken more easily by the turtle's beak than in bigger prey individuals, leading to a preference of turtles for smaller crayfish and mussels. Furthermore, we hypothesised that turtles, as poikilothermic organisms, are more active during sun exposure, and prey more often and faster on zebra mussels when exposed to sunlight. To verify this, half of the prey choice tests with zebra mussels were carried out in the sun. The results of this study can provide important information on the feeding behaviour of the European pond turtle and whether the reintroduced turtle can potentially have a positive influence on the wetland ecosystem, not only as an umbrella species for other locally threatened species, but also as a potential natural predator of invasive non-native invertebrate populations.

Methods

Study site

The study site Neu-Woerr is located in the middle of the Upper Rhine Valley, at the border between the towns of Lauterbourg (most northern location of Alsace, France) and Neuburg am Rhein (most southern location of Rhineland–Palatinate, Germany, Fig. 1). Since the channelisation of the Rhine in the second half of the 19th century, the oxbow lakes with their silting zones, marsh, reeds, and dead wood prevail, yet they are surrounded by an area of settlement, agricultural land, and riparian forests. Since 2000, major wetland management has been carried out to create a suitable habitat for the reintroduction of the European pond turtle (Philippot and Georges 2023). This consisted in creating a network of ponds over a 4 km wide area connecting existing drowned trenches in Germany to a formerly exploited gravel pond in France, surrounded by newly created small ponds connected to the ground water. Since 2013, about 650 European pond turtles have been released (~550 in France, ~100 in Germany) by local authorities and NGOs.

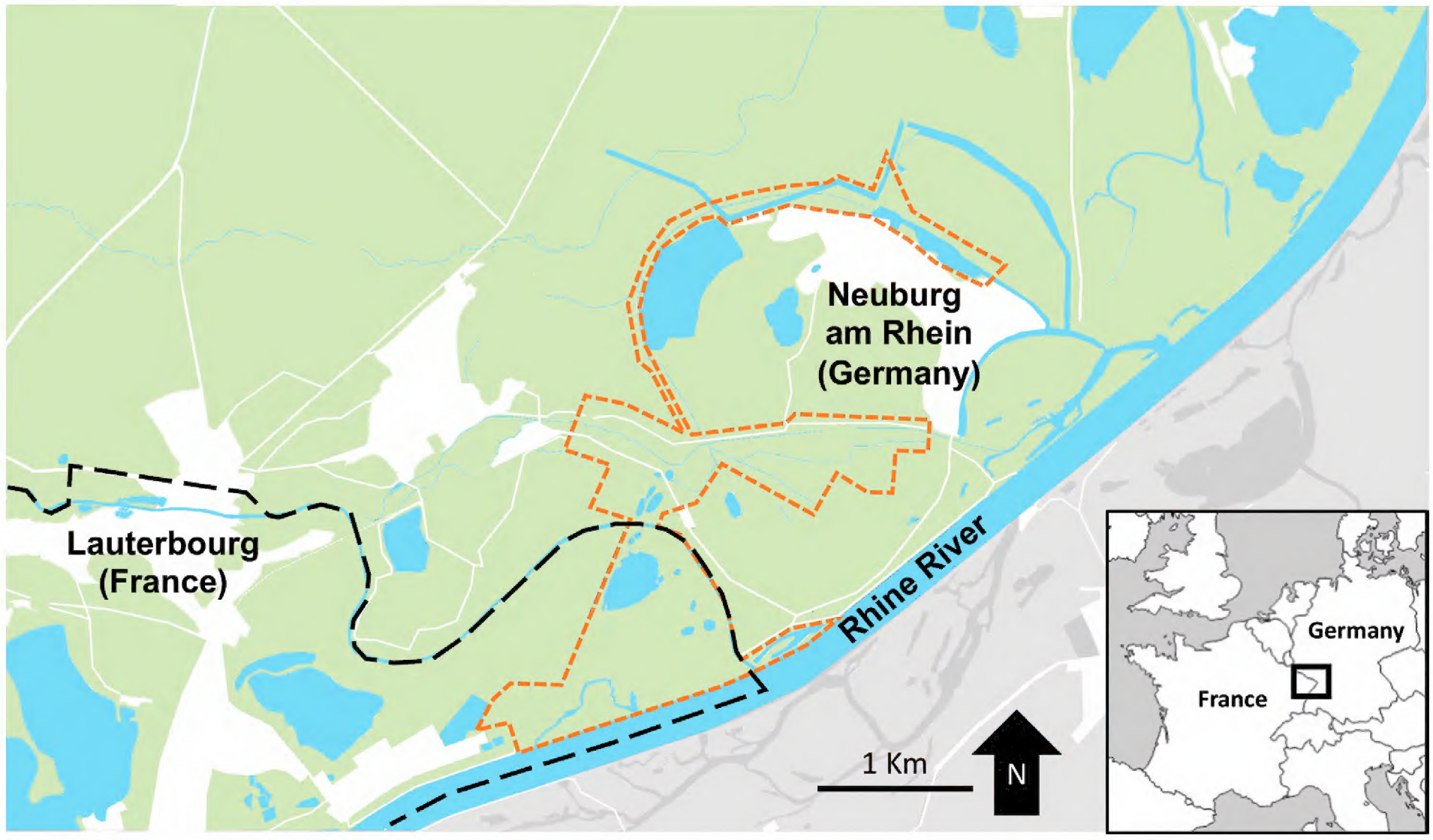

Figure 1. Simplified map of the study site Neu-Woerr (orange dashed line), at the border (black dashed line) between France and Germany where the pondscape has been restored prior reintroduction of European pond turtles (*Emys orbicularis*; blue: water bodies, green: natural and agricultural landscapes, white: artificial landscapes). Map was created with Plans (version 3.0) based on OpenStreetMap data.

Turtle predation on calico crayfish - faecal analysis

Faecal samples were collected in Neuburg where the calico crayfish occurs, but the zebra mussel has not yet been detected. During the monitoring of the turtle population in 2021, consisting of monthly trapping sessions of five successive days between April and October, 19 turtles captured in Neuburg were placed separately in 64-litre plastic boxes (60 × 40 × 32 cm). In addition to sex determination, each turtle was measured with a digital calliper (standard carapace length, ± 1 mm) and weighed with a balance (body mass, ± 1 g). Lukewarm (~25 °C) tap water was added to stimulate the intestine activity. As soon as a turtle defecated, the faeces were collected with a spoon or a fine filter sieve, stored in a plastic tube, and directly frozen at -20 °C in the field, and frozen at -80 °C in the laboratory. If a turtle did not defecate within the first hours, the water was changed as soon as it had cooled down with fresh lukewarm tap water. If a turtle did not defecate after two days, the faecal sample collection was cancelled to start with the prey choice test with calico crayfish caught as bycatch during the turtle monitoring (see below). Only faecal samples taken before the prey choice test with calico crayfish were used to analyse the potential crayfish eDNA in faeces.

In the laboratory, each faecal sample was homogenised by grinding to fine powder using a mortar and liquid nitrogen. Before being reused, the mortar and pestle were decontaminated in a bath of 10% bleach for 30 minutes, followed by a rinsing with 70% denatured ethanol and UV irradiation for 15 minutes (Ducotterd et al. 2020). Approximately 100 µg (variations ranging from 84 µg up to 201 µg depending on the amount of faecal material and frozen water residues) of the resulting fine powder was then used for the genomic DNA extraction. The extraction was performed with the Qiagen QIAamp PowerFecal Pro DNA Kit (Qiagen N.V.,

Venlo, Netherlands) following the manufacturer's protocol (Ducotterd et al. 2020). Using the Qiagen Type-it Microsatellite PCR Kit, a PCR Master Mix with specific calico crayfish primers Imm_COI_76F (forward: 5'-GAATAGTTGGGACTTC-GTTAAGAT-3') and Imm_COI_516R (reverse: 5'-CTGCACGTATATTA-ATAGCCGT-3') was prepared (Chucholl et al. 2021). 10 µL of the PCR Master Mix and 2 µL of the extracted DNA were mixed per sample tube. A positive and a negative control were added to exclude false positive and false negative results. The negative control consisted of water; the positive control contained calico DNA diluted with water (1:3). The Thermocycler Primus 96 advanced (PEQLAB) was used with the following cycling profile: initial denaturation at 95 °C for 15 min, followed by 30 cycles of 94 °C for 30 sec, 54 °C for 90 sec and 72 °C for 60 sec, and a final extension at 60 °C for 30 min. Presence or absence of calico crayfish DNA in the faecal samples was finally confirmed on a 1.5% agarose gel.

Prey choice test with calico crayfish

The prey choice tests of turtles on calico crayfish were carried out during the turtle monitoring on the Neuburg field site from May until October 2021. The prey choice tests were performed directly after the collection of faecal samples, because the turtles had already been acclimatised in the boxes. The turtles were not provided with any new feed. Crayfish were captured as bycatch in the traps used for the turtle monitoring. Upon capture, calico crayfish specimens were identified at the species level thanks to the tuft of hair in the inside of the chelipeds and the pattern of black lines on the abdomen (Collas et al. 2012). In addition to sex determination, each calico crayfish was measured with a digital calliper (cephalothorax length, from the tip of the rostrum to the end of the cephalothorax, ± 1 mm) and weighed with a balance (body mass ± 1 g). The number of chelipeds was counted, and the hardness of the shell was determined: the carapace was distinguished between the normal status 'hard' and directly after moulting as 'soft'. For each of the 11 trials, one 64-litre plastic box was filled with 5 cm of lukewarm (~20 °C) fresh tap water, as the European pond turtle has been reported to preferentially feed under water (Kummer et al. 2017). Taking turtles' habits into consideration, a basking stone was added, and one side of the box was slightly elevated to create one part of the box with more and the second part of the box with almost no water. One single turtle was placed in one prepared box together with six calico crayfish, three males and three females, each of the size categories: small (cephalothorax ≤ 25 mm), medium (25–35 mm), and large (≥ 35 mm).

Within the first half hour of the trial, all visible interactions focusing on feeding and defending attempts between turtles and crayfish were recorded. Then the boxes were checked at least every four hours, except at night-time, for possible crayfish cannibalism attempts and changes in the crayfish status according to six categories: (0) **Disappeared**: individuals that could not be found anymore in the box. (1) **Remains**: only parts of the body remained. (2) **Attacked**: individuals alive, but with new wounds or missing appendages (chelipeds, antennae or legs). 3) **Dead**: individuals showing no sign of life, yet with an intact body. (4) **Weak**: individuals becoming inactive and neither fled nor defended themselves. (5) **Intact**: individuals whose body was visually unchanged. Status (0) and (1) were counted as proof of predation of calico crayfish by the European pond turtle and combined

for analysis. Status (2), (3), (4) and (5) were combined as not consumed. The prey choice tests were carried out for an average of 44 hours and a maximum of three days. The maximum duration of three days was not possible for every trial, as some turtles were only caught towards the end of the field week. Afterwards, the turtles were released at their exact capture location.

Prey choice test with zebra mussel

The prey choice tests with the European pond turtle and zebra mussels were carried out in summer 2014 at Mulhouse zoo (France). Ten turtles were used for the experiments, which were commonly presented to the public and have not yet been fed with zebra mussels at the zoo. The turtles were measured with digital calliper (standard carapace length, ± 1 mm) and weighed with a balance (body mass, ± 1 g). The mussels were collected in the largest water body (gravel pond, Fig. 1) on the French side attached to hard substrate (stones, wood) and were individually measured with a digital calliper (shell length, ± 0.1 mm) while still attached to the substrate. Each of the ten turtles was placed in a 64-litre box, where they were not fed for one day before the experiment started. For the experiment, five zebra mussels of different shell lengths, ranging from as small as possible via several intermediate stages to as large as possible. Tap water was added to each box, as in the crayfish experiment described above. The ten trials started simultaneously outside in a quiet place out of the public area, with five trials under sun and five in the shade of trees. The boxes were checked for four days at 8 a.m. and 6 p.m. for possible changes in the mussel status according to three categories: (0) **Disappeared:** individuals that could not be found in the box. (1) **Remains:** only parts of the body remained. (2) **Intact:** individuals whose body was visually unchanged. Status (0) and (1) were counted as proof of predation of zebra mussels by the European pond turtle and combined for analysis. After three days without additional feeding, the test was repeated once more with the same ten turtles and freshly dead mussels, which died due to suboptimal storage conditions, yet without external injuries. This allowed us to compare the feeding behaviour of the European pond turtle regarding living and dead prey.

Statistical analysis

We performed generalised linear mixed models (GLMMs) with binomial family and logit link function using the "lme4" package v. 1.1-33 (Bates et al. 2015) in R v. 4.3.1 (R Core Team 2023). We tested the effect of crayfish cephalothorax length, hardness (hard/soft) and sex (female/male) on crayfish consumption and the effect of cephalothorax length only as the p-value of this variable was striking in the full model. We further tested the effect of mussel shell length and sun exposure (sun/shade) on mussel consumption using a GLMM separately for living and dead mussels. Consumed (partly or fully eaten) calico crayfish and zebra mussel individuals were given the value 1, whereas those that were not consumed were given the value 0. We checked over/underdispersion with the "testDispersion" function from the "DHARMa" package v. 0.4.7 (Hartig 2024) and added turtle ID as random factor to all models, as each turtle was offered several crayfish or mussels.

For the models with living and dead mussels as dependent variables, we performed model selection using the "drop1" function. The function performs an

analysis of deviance test by removing each variable in turn. We then re-fitted the model by excluding the least significant explanatory variable with the highest p-value from the model so that only variables with $p < 0.05$ remained in the model. We have calculated the conditional R^2 for the models as we have fixed and random effects in the model using the MuMIn package v. 1.47.5 (Bartoń 2023). For living and dead mussels, we also performed survival analyses to compare trials in the shade and in the sun, using the time in days until each mussel was eaten as a predictor variable. We ran the Kaplan-Meier estimator with the survfit() and Surv() functions of the package "survival" (Therneau 2024). We further tested with Spearman correlations whether the turtles' carapace length correlates with the shell length of the largest consumed living and dead mussel. Assumptions for normality were tested prior using Shapiro-Wilk test and for linearity with scatterplots. The level of significance was $\alpha = 0.05$ for all models and the null hypothesis was rejected at $p < 0.05$.

Results

Turtle-predation on calico crayfish - faecal analysis

Faecal samples from 19 European pond turtles captured in the release site in Germany were collected and analysed (mean carapace length CL = 111.9 ± 23.6 mm, range 76–156 mm; Table 1). Three (two females and one immature) out of the 19 wild-caught turtles (15.8%) contained calico crayfish DNA in their faecal samples. Calico crayfish DNA was only detected in faeces collected in the summer months of June to August.

Prey choice test with calico crayfish

In total, 11 calico crayfish prey choice tests were conducted with 11 out of the 19 different turtles captured in Neuburg (Table 1). The mean cephalothorax length of all calico crayfish used in the prey choice test was 30.0 ± 6.5 mm (range 17–43 mm, n = 66). The mean cephalothorax length of small crayfish was 22.6 ± 2.2 mm (range 17–25 mm, n = 22), of medium crayfish 29.8 ± 2.3 mm (range 26–34 mm, n = 22) and of large crayfish 37.5 ± 2.1 (range 36–43, n = 22).

After the trial conduction, seven out of 66 calico crayfish (10.6%) were consumed by five different turtles (category 'remains' or 'disappeared'; Suppl. material 1: table S1). Turtles preyed on both male (4 out of 33, i.e., 12.1%) and female crayfish (3 out of 33, i.e., 9.1%). Yet, turtles preyed more often on soft crayfish (3 out of 9 soft items, i.e., 33.3%) than on hard crayfish (4 out of 57 hard items, i.e., 7.0%; Fig. 2). Regarding prey size, turtles tended to prey more often on small crayfish (5 out of 22, i.e., 22.7%) than on medium (1 out of 22, i.e., 4.5%) or large crayfish (1 out of 22, i.e., 4.5%; Fig. 2).

There was no significant effect of calico crayfish cephalothorax length, hardness and sex on the probability of being consumed in the full model (Suppl. material 1: table S2). When running a logistic regression with only cephalothorax length as a predictor variable, length had a significant negative effect, with small crayfish ($z = -1.988$, $p = 0.047$) being more prone to predation by European pond turtles (Fig. 3). The model with length only explained 30.7% of the variance (R^2c) in the data.

Table 1. Biometrics of European pond turtles (*Emys orbicularis*) used for eDNA analysis and prey choice tests in 2021. Turtles with positive and negative calico crayfish (*Faxonius immunis*) faecal eDNA are marked as eDNA+ and eDNA-, respectively. Individuals marked with an asterisk were used for the prey choice test after the faecal sampling. Individuals marked with two asterisks preyed on crayfish during the prey choice test. The unchipped immature turtle was a wild born individual originating from reintroduced adults, as confirmed by microsatellite analyses (Theissinger, unpublished data).

Turtle ID (PIT)	Sex	Body mass (g)	Carapace length (mm)	Capture date	eDNA
405926	Female	700	156	13 May	–
405758**	Female	410	120	6 July	–
404262	Female	479	134	7 June	–
403714	Female	567	134	9 June	+
237358	Female	238	105	6 Aug.	–
237211**	Female	185	95	29 Aug.	–
237137*	Female	163	92	6 Aug.	+
237072*	Female	189	95	31 Aug.	–
401954	Male	421	140	10 June	–
400194**	Male	377	136	8 June	–
399795	Male	332	128	11 May	–
397765	Male	346	127	11 May	–
394956**	Male	324	126	8 June	–
238210**	Male	148	93	29 Aug.	–
237187*	Male	245	116	29 Sept.	–
237280*	immature	83	76	1 Aug.	+
237330*	immature	158	87	31 Aug.	–
237070*	immature	152	88	30 Sept.	–
unchipped	immature	84	78	10 July	–

Prey choice test with zebra mussels

In total, 20 zebra mussel prey choice tests were conducted with ten turtles (mean carapace length = 123.1 ± 15.4 mm, range 102–148 mm; Suppl. material 1: table S3). The mean shell length of all mussels used in the prey choice test was 19.0 ± 6.2 mm (range 8–31 mm, n = 100). The mean shell length of all living mussels was 19.5 ± 6.6 mm (range 8–31 mm, n = 50). The mean shell length of all dead mussels was 18.6 ± 5.9 mm (range 8–27 mm, n = 50).

After the trial conduction, 47 out of 100 zebra mussels (47.0%) were consumed by the ten turtles in 16 out of 20 trials (80.0%). For the living mussels, 11 out of 50 mussels (22.0%) were consumed in 6 out of the 10 trials (60.0%). For the dead mussels, 36 out of 50 mussels (72.0%) were consumed in 10 out of 10 trials (100.0%). We found no significant difference in the survival probability between trials in shade and in sun for living mussels (χ^2 = 2.6, p = 0.1) and for dead mussels (χ^2 = 2.2, p = 0.1; Fig. 3).

After removal of the non-significant variable "sun exposure", there was a significant effect of mussel shell length on the probability of being consumed, with small mussels being more susceptible to predation by European pond turtles (z = -2.540, p = 0.011; Fig. 4). The final model explained 44.6% of the variance in the data (R^2c). There was no correlation between the turtle carapace length and the shell length of the largest living mussel that each turtle consumed (r = 0.029, n = 6, p = 1). Living mussels larger than 21 mm shell length were not predated by turtles.

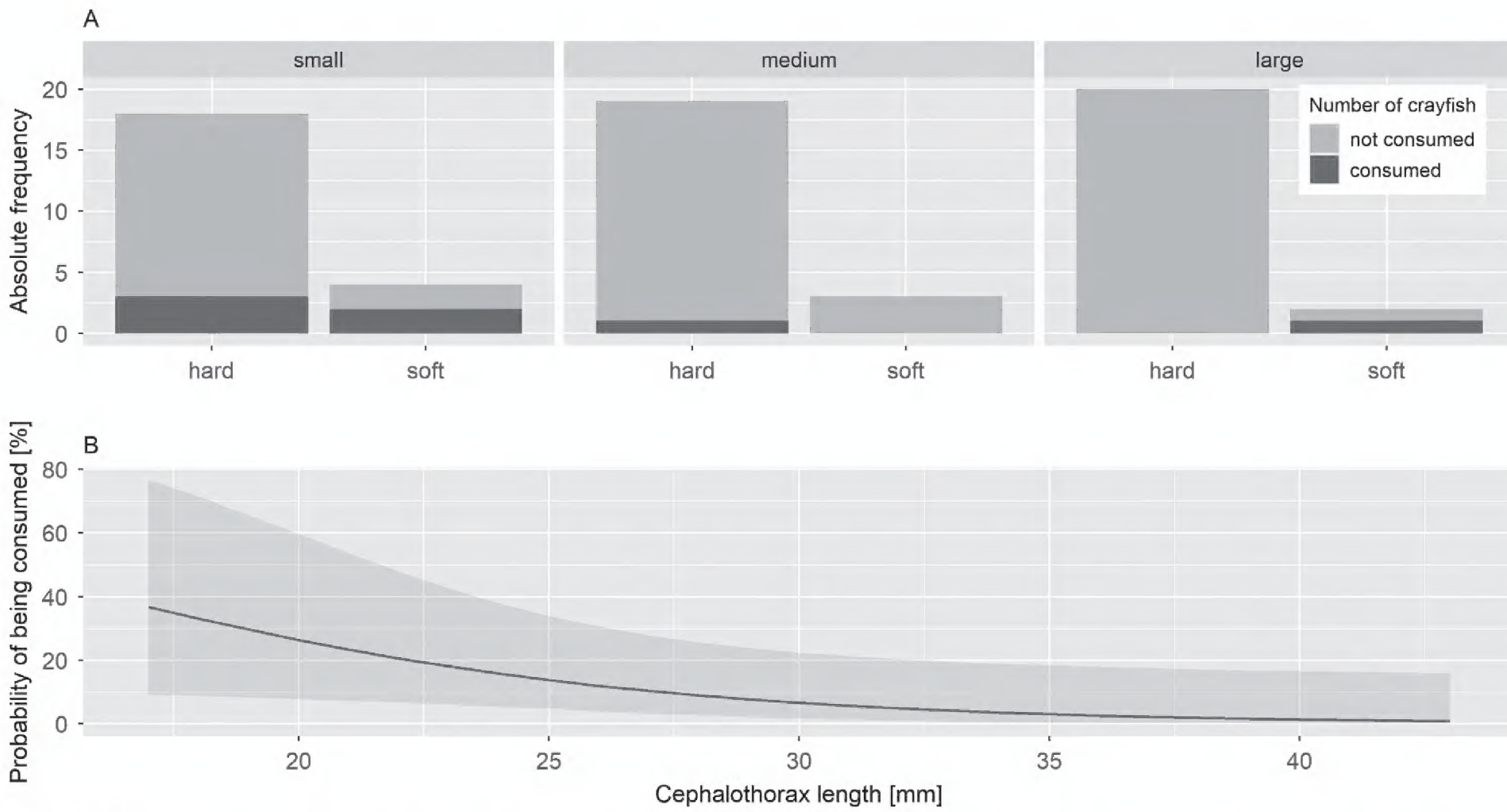

Figure 2. A. Number of calico crayfish (*Faxonius immunis*) consumed *vs.* not consumed per size (small, medium, large) and cephalothorax hardness (hard, soft), during feeding trials by European pond turtles (*Emys orbicularis*); **B.** Predation probability for calico crayfish in relation to cephalothorax length during feeding trials by European pond turtles. Shadow areas represent 95% confidence interval.

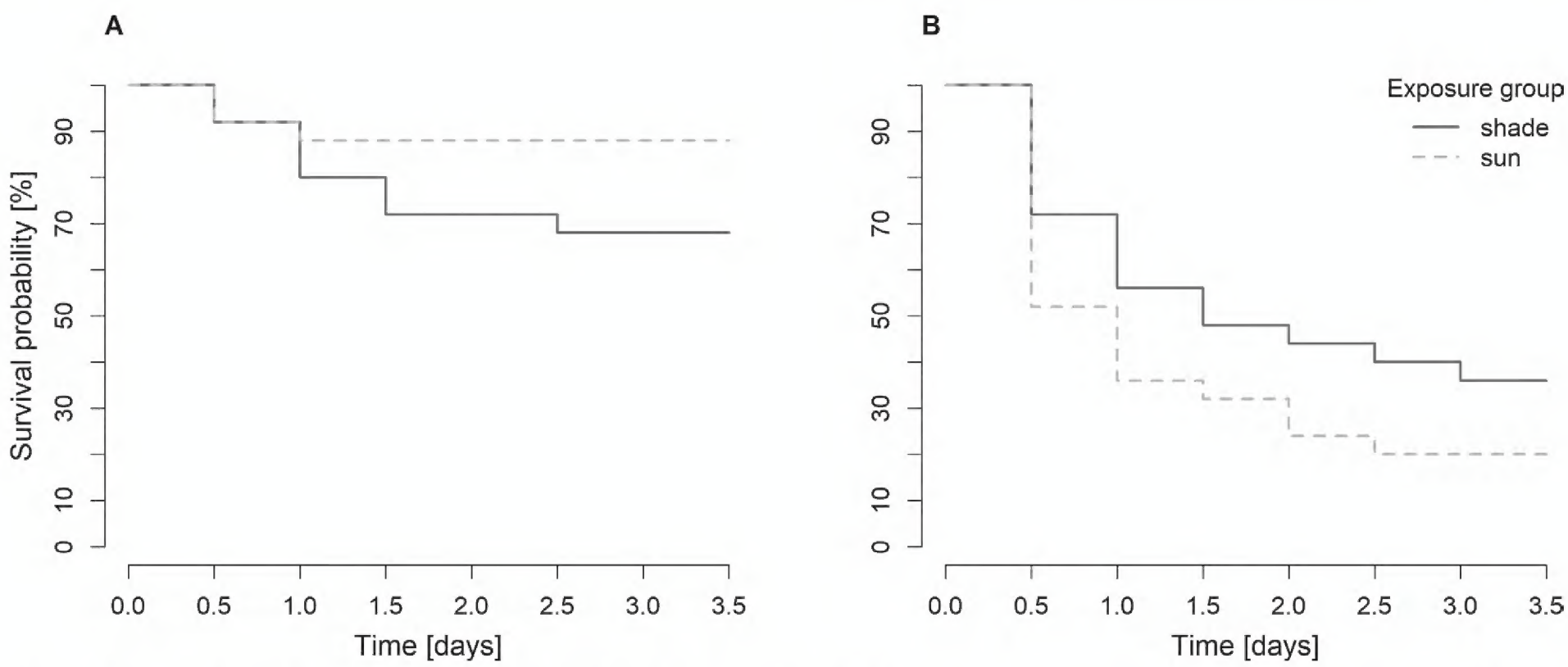

Figure 3. Survival probabilities for living (**A**) and dead (**B**) zebra mussels (*Dreissena polymorpha*) over time (days) during feeding trials by European pond turtles (*Emys orbicularis*). Survival is differentiated in the two exposure groups shade (dark grey) and sun (dashed line in light grey).

In all ten trials with dead mussels, at least one zebra mussel was consumed. After removal of the non-significant term "sun exposure", there was a significant effect of mussel shell length on the probability of being consumed, with small mussels being more susceptible to predation ($z = -3.191$, $p = 0.001$; Fig. 4). Yet, turtles were capable of preying on the largest dead mussels. The final model explained 44.3% of the variance in the data (R^2c), while the random effect (turtle ID) explained no additional variance. There was no correlation between the turtle carapace length and the shell length of the largest dead mussel that each turtle consumed ($r = -0.151$, $n = 10$, $p = 0.682$).

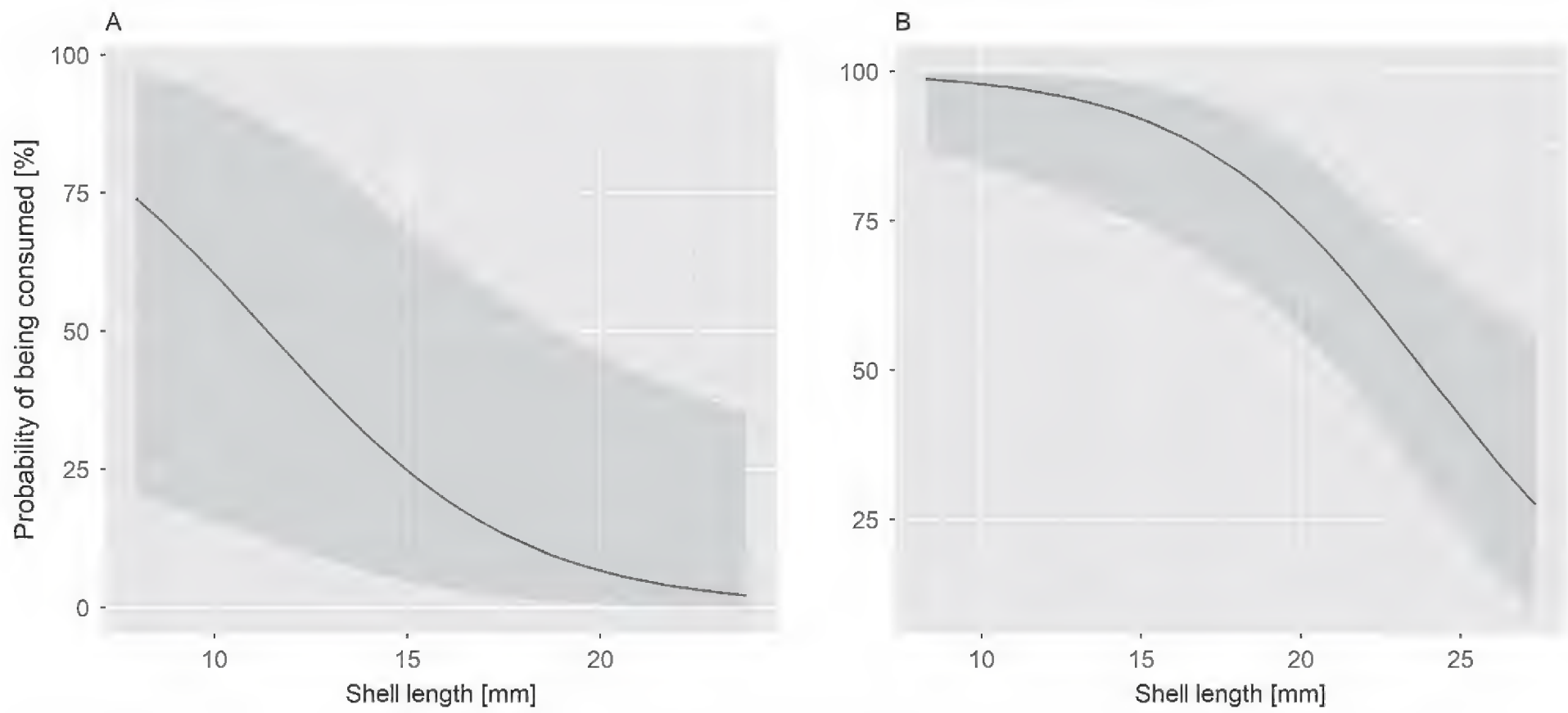

Figure 4. Predation probability for living (**A**) and dead (**B**) zebra mussels (*Dreissena polymorpha*) in relation to their shell length during feeding trials by European pond turtles (*Emys orbicularis*). Shadow area represents 95% confidence interval.

Discussion

This study provides new insights into the trophic interactions between the native European pond turtle and two non-native invertebrates which are highly invasive in the Upper Rhine Valley: the calico crayfish and the zebra mussel. The three species can potentially meet and interact with each other in the wild, as they are either subject of reintroduction or recent invasive expansion in the Upper Rhine Valley, including the Neu-Woerr site where this study was partly run. The results of our study proved that the European pond turtle preys on both studied invasive invertebrates in captivity and on calico crayfish also in the wild. As these invasive non-native species cause great ecological and economic damages, this study provides valuable empirical data about their trophic relationship with the European pond turtle and the turtle's potential role as a new predator of invasive non-native calico crayfish and zebra mussels.

In more than 15% of the examined reintroduced turtles captured in the wild, calico crayfish DNA was detected in the faeces. Faecal samples are only a snapshot of a turtle's last food intake. Indeed, one turtle (404262) found with no calico DNA in its faeces in June (Table 1) was recaptured in July with calico DNA in its faeces (data not shown), which would increase this value to 21%. Considering the opportunistic feeding habit of the European pond turtle, our finding indicates that turtles do quite regularly consume calico crayfish in the wild. Our results fit with a previous study in Southern France, where wild adult European pond turtles have been reported to prey on the red swamp crayfish (*P. clarkii*), another invasive non-native crayfish species in Europe, yet without mentioning whether prey was consumed dead or alive (Ottonello et al. 2005). Positive and negative faecal samples were obtained from turtles caught with or without crayfish in the same trap. We cannot say for sure whether a trap without calico crayfish originally contained one that was eaten by the turtle before we emptied the trap. However, other studies have shown that the gastrointestinal transit time in turtles was several days (Valente et al. 2008; Olayinka-Adefemi et al. 2017) and therefore the calico crayfish potentially eaten in the traps should not yet be present in the faecal samples.

Importantly, our study shows that turtles with calico crayfish DNA in their faeces were representative of the entire size range of individuals released in the study site, including adults and immatures.

We found that the European pond turtles used in the experiment preferred preying on small calico crayfish: the smaller the crayfish, the higher the probability of being consumed by the turtle. This can be explained by the fact that smaller crayfish are less equipped to defend themselves against predators, because of smaller claws, lowered mechanical resistance of carapace to the turtle's beak, and lowered physiological conditions related to the recent moulting. In crayfish, where the exoskeleton is hard and inflexible, growth is only possible by moulting. According to Andrews (1907), the spiny-cheek crayfish (*Faxonius limosus* Rafinesque, 1817), which is a congener of the calico crayfish, moults between 7 to 12 times during its first summer and less frequently the following years when it becomes mature (cephalothorax length > 25 mm; Rach and Dawson 1991). Small crayfish have therefore less time to develop a thick shell compared to medium and large crayfish (Bielawski 1971) and are generally easier to bite through for turtles. Preying on small individuals is therefore more profitable for the turtles, yet requires more prey items to fill food requirements compared to larger prey. Aquiloni et al. (2010) came to the same conclusion concerning the crayfish size in a study investigating the predator-prey relationship between the European eel (*Anguilla anguilla* Linnaeus, 1758) and the invasive non-native red swamp crayfish (*P. clarkii*). Since smaller crayfish lose the intraspecific competition for the best shelters against larger crayfish (Garvey et al. 1994), it is likely that smaller crayfish are available to the turtles as prey in the wild, at least in water sections where shelters are limited.

Since the trials could not be observed continuously, cannibalism among crayfish cannot be completely ruled out. However, it is highly unlikely that cannibalism was the cause of disappearance for crayfish of the categories 0 (disappeared) and 1 (remains). This is because in four out of five prey choice tests, feeding attacks by the turtle were directly observed, and most of the crayfish of these two categories were eaten within the first four hours, with the latest consumption occurring after two days. This time span is very short compared with another experiment, in which smaller *P. clarkii* individuals were fully consumed within ten days by larger *P. clarkii* individuals that had previously been starved for 15 days (Ibrahim et al. 1995). Additionally, the crayfish in our study were mostly taken fresh from the traps (not starved), and not only small crayfish but also one medium and one large crayfish were consumed. However, for the ten crayfish that were assigned to category 2 (attacked) at the end of the experiments, it is not possible to distinguish whether the wounds or missing appendages were caused by attacks by turtles or by cannibalistic attacks by other crayfish.

Direct observations of the prey choice trials indicated that crayfish do not seem to be an easy prey for turtles in general. Kummer et al. (2017) showed that the European pond turtle has a low variation in food intake following a stereotypical pattern. The turtle is therefore not able to react directly to moving prey, and crayfish might manage to escape or to hide. In the boxes of the prey choice test, however, escaping and hiding was limited to some extent for the crayfish, so the turtles might have been more successful in captivity than they are in the wild. Although pond turtles equally preyed on female and male crayfish in our setting, they may also face anti-predator aggressive behaviours from male crayfish, which have been reported to be more aggressive than females (Chucholl et al. 2008). To be able to exclude external factors influencing the feeding habits of the turtles, follow-up studies need

to be carried out under conditions where, e.g., light, temperature, potential shelters for crayfish and the turtles' state of hunger, sex and size are considered.

Regarding the other invasive species, the zebra mussel, our prey choice tests demonstrated that six out of ten turtles consumed at least one living mussel: the probability with which living zebra mussels were consumed was about 50% higher for individuals smaller than 15 mm. A possible explanation why turtles prefer to prey on small mussels could be the thickness of the shell more than the shell size itself. Because the shell of small mussels has accumulated less calcium carbonate (Chakraborty et al. 2020), it is thinner and easier to break. Prejs et al. (1990) reported similar results with the roach (*Rutilus rutilus* Linnaeus, 1758) preying on small-sized zebra mussels. Consumed dead mussels were on average larger than consumed living mussels, suggesting that beside shell hardness, mussels prevent predation by pulling resistance that permits closing their shell and by attaching to the substrate in large aggregates (Robson et al. 2007). The fact that the size of the turtles did not correlate with the size of the largest mussel eaten may be due to the fact that the turtles in the mussel trials were of very similar size.

Contrary to our hypothesis, sun exposure had no impact on the prey catching efficiency of the European pond turtle on zebra mussels: the survival probability for living and dead mussels in shade and in sun did not significantly differ. The European pond turtle did not search more actively for food, nor did the turtle prey on mussels within a shorter period of time under sun exposure where temperature is higher. These findings fit with Marchand et al. (2021) who suggested that the European pond turtle forages in the morning, whereas warmer periods of the day are used for sun basking and digestion. The fact that no difference in the feeding behaviour between sun and shade was found could thus be due to the daily pattern in turtle's behaviour. In our setting, in the morning, when turtles usually forage, both experimental set-ups were still exposed to similar sun conditions and temperatures. Around noon, the turtles then digest either in sun or in shade. In this case, the sun only has an influence on how quickly the turtle digests, as the metabolism is faster at higher temperatures.

Comparing the mussel trials to the crayfish trials, relatively more turtles were actively preying on zebra mussels and more prey items were consumed: mussels were the easier prey in these two experimental set-ups, as they could not escape from the turtle while crayfish were observed doing so. In addition, the mussel trials were run with zoo animals which were putatively less stressed by being observed in the boxes, as they are used to captivity, in contrast to the wild turtles used for the crayfish trials. Nevertheless, the results of these prey choice tests can only partly be transferred to the wild. In the wild, the mussels attach to hard substrate for colonisation and often occur in large densities (Khalanski 1997), whereas crayfish are mobile individuals more prone to escape predators. Since small mussels are the most exposed in these mussel aggregations, they are generally also exposed to a higher predation pressure (Prejs et al. 1990). Furthermore, the pulling resistance of mussels correlates positively with the mussel size and is therefore lower for small mussels (Prejs et al. 1990). Thus, the probability that small mussels are consumed by turtles seems to be even higher in the wild. The collection of faecal samples of the European pond turtles and their analysis for zebra mussel DNA, as it was done for the calico crayfish in this study, could provide information about the feeding behaviour of the turtle in the wild, and whether the European pond turtle could potentially reduce zebra mussel populations.

This study shows that the native European pond turtle can prey on invasive non-native calico crayfish and zebra mussels. Yet the role of the turtle as potential biocontrol for these invasive species is highly debatable. According to Hajek and Eilenberg (2018) a predator may act as biocontrol when it has high searching skills for prey, high prey specificity and a high fecundity. This is why non-native species have commonly been used as biocontrol agents. The last two characteristics can hardly be attributed to the European pond turtle. Yet, compared to classical biological control agents, the European pond turtle has the advantage of being native to the habitat and therefore not being a threat for other native species. Under this condition, and in the context of reintroduction initiatives such as the one in the Neu-Woerr study site, the turtle as an umbrella species is an enrichment for the native ecosystem and additionally contributes as a new top-down predator to the control of the two investigated invasive non-native species, even if the turtle may not be efficient as biological control.

However, the turtle's contribution for biocontrol could be important, since other control methods for the zebra mussel are limited and unsatisfactory in open water bodies (Strayer 2009), like the ponds and oxbow lakes on the French side of the Neu-Woerr study site, where the zebra mussel has already been detected (Grac et al. 2015). Compared to the zebra mussel, the calico crayfish has already spread throughout the whole French-German turtle reintroduction area of Neu-Woerr. To control invasive crayfish, whose stocks were once even promoted in several cases for economic gains in fishery ignoring the consequences for native species and European aquatic ecosystems (Jussila et al. 2021; Theissinger et al. 2022), various methods have already been tested. For instance, in their assessment of feasibility and effectiveness of different management strategies for the Rhine-Meuse River District, Lemmers et al. (2021) reported from the literature that enhancing ecological robustness and resilience of water systems were the highest ranked mitigations. Accordingly, insufficient top-down regulation by predators would facilitate the spread of invasive non-native crayfish in the Rhine–Meuse River District (Lemmers et al. 2021). Consequently, the promotion of natural predators could reduce crayfish densities. In the USA, Rach and Bills (2011) noted a drastic decline in the calico crayfish population in a fish rearing impoundment after stocking with largemouth bass (*Micropterus salmoides* Lacépède, 1802). Whereas carnivorous species, like the largemouth bass, might have a bigger effect on the crayfish population compared to the European pond turtle with its opportunistic feeding behaviour, Hein et al. (2007) showed that trapping combined with the protection of crayfish predators can lead to a great decline in crayfish populations. Since the European pond turtle population size is still quite low in the Neu-Woerr study site, additional turtle releases and crayfish trapping might contribute to reducing the crayfish population size.

Finally, in the transbordering Neu-Woerr study site, the European pond turtle is also subject to competition by other highly invasive non-native species, the red-eared slider (*Trachemys scripta elegans* Wied-Neuwied, 1839) and the yellow-bellied slider (*Trachemys scripta scripta* Thunberg in Schoepff, 1792), and to predation by the also highly invasive raccoon (*Procyon lotor* Linnaeus, 1758; Georges and Theissinger, unpublished data). These species originate from North America and were intentionally introduced to Europe during the 20th century for pet trade (Kopecky et al. 2013) and for fur production (Müller-Using 1959), respectively. The pond sliders and the raccoon, as effective competitor and predator for juvenile and adult European pond turtles, respectively, may counteract the reintroduction efforts and hinder turtle population expansion (Cadi and Joly 2003; Polo-Cavia et al. 2011;

Balzani et al. 2016; Schindler et al. 2017; Karson et al. 2018; Kagayama et al. 2021). The extent to which their spread affects the population and reproductive success of the European pond turtle, which was demonstrated for the first time with a wild born individual in the course of this study (Table 1), needs to be investigated. Further, the pond sliders and, to an even larger extent, the raccoon may also act as a top-down invasive threat for many other species, such as native amphibians, reptiles, birds, and bats as well as for crayfish regardless their origin (Michler and Michler 2012). Control measures like hunting and trapping pond sliders and raccoons need enormous efforts and may not be accepted by the public since these two species are popular animals, especially among children (Winter 2009; Philippot et al. 2019). Awareness raising and education campaigns of the common public and the laypersons, including school children, retailers, fishermen and pet owners, regarding the huge damage these and other invasive species cause in native ecosystems, is essential for reducing the probability of non-native species release into the wild and for implementing appropriate mitigation measures (Salgado 2018; Meinard et al. 2022; Haubrock et al. 2025). The three-year socio–ecological research project Emys-R contributes to this goal by researching socially supported best practice methods of wetland restoration for the recovery of European biodiversity in transnational cooperation. Within this project, the European pond turtle is not only the focus of research as an umbrella species, but also as a potential flagship species to improve people's perception of nature, especially for wetlands.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported. Animal handling and experiments were in full compliance with local, national, ethical, and regulatory principles, under authorisations owned by Dr Vet Benoît Quintard in Mulhouse zoo and by JYG in the Neu-Woerr site (arrêté préfectoral delivered Sept 11, 2017 following protocols agreements by the French Ministry for National Education, Higher Education and Research and by the Ethical Committee for Animal Experimentation, CREMEAS, CEEA 35, Strasbourg, France).

Use of AI

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Author contributions

Conceptualization: IMK, BQ, KT, JYG; Methodology: IMK, BQ, KT, JYG; Investigation: IMK, BQ, KT, JYG; Data Curation: IMK, JYG; Formal analysis: IMK; Writing - Original draft: IMK; Writing - Review and Editing: IMK, BQ, KT, JYG; Visualization: IMK, JYG; Supervision: KT, JYG; Project administration: KT, JYG; Funding Acquisition: KT, JYG

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Additional information

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Data type: pdf

Explanation note: **table S1.** Number and proportion of calico crayfish (*Faxonius immunis*) status. **table S2.** Generalized linear mixed model parameter estimates of calico crayfish. **table S3.** Biometrics of European pond turtles (*Emys orbicularis*) used for prey choice tests on zebra mussels (*Dreissena polymorpha*).

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